水玉簪属系统发育重建的初步研究

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Phylogenetic reconstruction of *Burmannia* L.
(Burmanniaceae): a preliminary study

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Abstract　Preliminary cladistic analyses of the genus *Burmannia* were performed using different outgroups. Although results from different analyses were inconsistent in some aspects, some clades were found in both analyses, suggesting the specific relationships among species in these clades are well-solved. Of the two sections recognized by Jonker, sect. *Foliosa* is probably a monophyletic group, while sect. *Burmannia* is not. If the loss of chlorophyll is considered to be an irreversible process, holo-mycoheterotrophism has very likely emerged only once in the tribe Burmannieae.

Key words　*Burmannia*; Burmanniaceae; Cladistic analysis; Mycoheterotroph; Mycoheterotrophism

Jonker (1938) divided the genus *Burmannia* into two sections: sect. *Foliosa* has five species of autotrophs in the Americas and in Malesia; and sect. *Burmannia* has ca. 52 autotrophic and mycotrophic species. Members of the sect. *Foliosa* are rhizomatous perennials with numerous large, parallel-veined, ensiform, imbricate and decurrent green leaves on the lower part of the stems; and densely many-flowered inflorescences with wingless flowers or flowers with rather narrow perianth wings. In the other section, *Burmannia*, the autotrophic species possess a basal rosette with linear leaves and upward smaller cauline leaves, while the mycotrophic species lack basal rosette leaves, and the cauline leaves are appressed and scale-like. Although earlier authors' (Ridley, 1924, Engler, 1889) classification was based on the presence or absence of chlorophyll, Jonker (1938) considered that it was not sufficient to be the basis for a supraspecific classification. He noticed that of two closely related species one could be mycotrophic, and the other non-mycotrophic, while practically no difference exists in facies and floral morphology. In other mycotrophic angiosperm groups, the photosynthetic ability may have been lost more than once, as Kron (1996) reported for the Pyrolaceae-Monotropaceae group. The mycotrophic and non-mycotrophic taxa in this group are closely related to each other as suggested by morphological characters of vegetative and reproductive organs; the only difference between the chlorophyllous taxa and the achlorophyllous taxa is the presence or absence of chlorophyll (Henderson, 1919). Since the relationship between chlorophyllous and achlorophyllous taxa within this group is very similar to that in the Burmanniaceae, the loss of chlorophyll in this group has implication for a better understanding of the evolution of holo-mycotrophism in *Burmannia*.

Since of the OTUs covered in the present study, only the *Burmannia* species occurring in the Old World are based on a thorough and extensive taxonomic revision (Zhang & Saunders, 2000, 1999; Zhang, 1999), while data of the New World species and the other genera in the family are based on the study of very limited number of specimens or previously published work (Maas *et al*., 1986, Rübsamen, 1986), the objectives of this study are to test whether the two sections of the genus are monophyletic, to elucidate the phylogenetic relationships among species within the genus, and to elucidate the evolution of mycoheterotrophism (viz., the emergence of achlorophyllous species) in *Burmannia*. It is not specifically aimed at elucidating the relationships among genera in the family.

1 Materials and methods

1.1 The ingroup and the outgroup

1.1.1 Ingroup terminal taxa

Jonker (1938) divided the tribe Burmannieae Miers. into two subtribes, Euburmannieae (correctly Burmanninae) and Apterieae (correctly Apterinae), and included three genera, viz., *Burmannia* and two monotypic mycoheterotrophic genera *Campylosiphon* and *Hexapterella* in the subtribe Burmanninae. In the subtribe Apterinae he included six genera, viz., *Apteria*, *Cymbocarpa*, *Dictyostega*, *Gymnosiphon*, *Marthella*, and *Miersiella*. In the other tribe, Thismieae, he included six genera, that is, *Afrothismia*, *Geomitra*, *Glaziocharis*, *Scaphiophora*, *Thismia* and *Triscyphus*. *Thismia* is the largest genus among them. Because all genera in the family Burmanniaceae other than *Burmannia* are achlorophyllous mycoheterotrophs, while *Burmannia* is the only genus in the family having species with green leaves, whether they are sister taxa of, or only clades of *Burmannia* is uncertain. *Burmannia* could not be presumed to be a monophyletic group. A total of 57 species in the genus *Burmannia*, a representative species each from the eight genera in the tribe Burmannieae, and one representative species of the tribe Thismieae (*T. panamensis*) were included in the cladistic analysis. Only a few species in the genus *Burmannia*, namely, *B. bifaria*, *B. tridentata*, *B. liukiuensis* and *B. steenisii*, were not included because they are either poorly known or their validity as separate taxa is doubtful. The ingroup included 66 terminal taxa.

1.1.2 Outgroups

The most commonly applied method of determining the relative distributions of the states of the characters (the polarities) is the outgroup comparison method (Maddison *et al*., 1984, Watrous & Wheeler, 1981).

Cladistic analyses based on morphological data (Stevenson & Loconte, 1995), as well as a combined morphological and molecular data (Chase *et al*., 1995, 1993), revealed that the family Burmanniaceae is most closely related to the family Corsiaceae, a mycoheterotrophic family of 3 genera disjunctly distributed in South America, Australasia and China (Zhang *et al*., 1999; Ibisch *et al*., 1996; Van Royen, 1972). A representative species (*Corsia lamellata*) from the family Corsiaceae is chosen as the outgroup. The family Burmanniaceae is also related to the family Orchidaceae, as demonstrated by morphological (Stevenson & Loconte, 1995, Cronquist, 1988, Dahlgren, 1985, 1982) as well as embryological studies (Rübsamen, 1986). As the habit of mycoheterotrophism in the Burmanniaceae and the Corsiaceae could have originated convergently, a representative autotrophic species (*Habenaria* sp.) of the family Orchidaceae is also included as an alternative outgroup.

The data matrix includes 66 ingroup taxa and two outgroup taxa, with 61 morphological characters (Table 1).

Table 1　Taxa and coded characters for the cladistic analysis of *Burmannia*.
Burmannia data with 68 taxa and 61 characters

Taxa (68)\Characters(61)

Habenaria sp.

Corsia lamellata

Thismia panamensis

Campylosiphon purpurascens

Hexapterella gentianoides

Cymbocarpa refracta

Gymnosiphon usambaricus

Aptera setacea

Miersiella umbellata

Dictyostega orobanchoides

Marthella trinitatis

longifolia

foliosa

kalbreyeri

Table 1 (continued)

polygaloides	0 0 1 0 1 1 0 0 0 0 0 0 0 1 1 0 0 0 1 1 0 0 0 1 0 0 0 0 0 0 0 0 0 - 1 1 1 0 0 0 - 1 1 0 1 0 1 1 1
compacta	0 0 1 0 1 1 0 0 0 0 0 0 2 1 0 1 0 0 1 1 0 0 0 6 1 0 0 0 1 0 0 0 0 1 2 1 0 1 0 0 1 1 0 0 0 0 0 0 1
capitata	1 0 1 1 - 0 1 1 1 2 1 0 1 1 0 1 1 0 1 0 0 1 1 1 0 0 0 0 1 0 0 0 1 0 - 1 1 1 1 0 0 - 1 1 1 0 1 1 1
alba	1 0 1 1 - 2 - 1 2 1 2 1 1 0 0 1 1 0 1 0 1 0 1 1 0 0 0 0 ? 0 0 0 0 0 - 1 1 0 0 0 - 2 1 1 0 1 1 1 1
grandiflora	1 0 1 1 - 2 - 1 2 1 2 1 1 0 0 1 1 0 1 0 1 0 1 1 0 0 0 2 6 1 0 0 0 0 1 1 0 1 0 0 0 - 2 1 1 0 1 0 0 1
dasyantha	1 0 1 1 - 2 - 1 2 1 2 1 1 0 0 1 1 0 0 0 1 0 1 1 0 0 0 0 2 6 1 0 0 0 1 1 1 1 1 0 0 - 2 1 1 0 1 0 1 0 1
tenella	1 0 1 1 - 0 1 0 0 0 0 0 7 1 0 0 0 1 0 0 0 0 1 0 0 0 0 2 1 0 0 1 0 ? 1 1 0 1 0 0 0 0 1 1 0 0 1 1 1
biflora	1 1 1 1 - 2 - 1 2 1 3 1 1 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 3 1 0 0 1 0 1 1 0 1 0 0 0 1 1 0 0 0 0 0 1
damazii	1 0 1 1 - 2 - 1 2 1 2 1 2 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 5 1 0 0 0 1 0 1 0 1 0 1 0 1 1 1 0 0 0 0 1
australis	1 0 ? 1 - 2 - 1 2 1 2 1 1 0 0 0 5 0 0 1 0 1 0 1 0 0 0 2 1 1 0 0 0 0 2 1 1 0 0 2 0 2 1 1 0 1 0 1 1
flava	1 0 1 1 - 0 0 0 1 2 1 1 ? 0 0 1 0 0 0 0 0 1 0 1 0 0 0 2 1 0 0 0 0 0 1 0 1 0 1 0 2 1 ? 1 0 0 1 0 1
tenera	1 0 1 1 - 1 2 1 2 1 2 1 1 ? 0 0 0 1 0 0 0 1 0 1 0 0 0 6 1 0 0 0 0 0 2 1 0 1 0 0 2 0 2 1 ? 1 0 0 1 1
stuebelii	1 0 0 1 - 0 1 2 1 2 1 2 1 2 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 2 1 0 1 0 0 2 0 0 1 1 0 1 0 1
aprica	0 0 0 1 - 0 1 0 0 ? 0 0 0 0 0 0 1 0 0 0 1 0 1 0 0 0 0 ? 1 0 0 0 0 0 2 1 0 1 0 0 2 0 ? 1 1 0 1 0 0 1
bicolor	1 0 0 1 - 0 1 0 1 0 1 1 0 1 0 0 1 0 0 0 1 0 1 0 0 0 0 1 1 0 0 0 0 0 2 1 0 1 0 0 2 0 ? 1 1 0 1 0 1 1
jonkeri	1 0 0 1 - 0 1 1 ? 1 2 1 ? 0 0 0 0 0 0 0 1 0 1 0 0 0 0 1 1 0 0 0 0 0 2 1 0 1 0 0 2 0 1 1 1 0 1 0 1 1
sanariapoana	1 0 1 1 - 2 - 1 2 1 2 1 1 0 0 1 0 1 0 1 0 1 0 1 0 0 0 6 1 0 0 0 0 0 1 1 0 1 0 0 1 0 1 1 1 0 1 0 1 1
vaupesana	1 0 0 1 - 0 0 0 1 2 1 1 0 0 0 0 1 0 1 0 1 0 1 0 0 0 0 6 1 0 0 0 0 0 1 1 0 1 0 0 1 0 0 1 1 0 1 0 1 1

Table 1 (continued)

hexaptera
1 1 1 1 - 2 - 1 2 1 ? 1 2 2 0 3 - 1 0 0 0 1 0 1 1 0 0 0 0 0 1 1 0 0 0 0 1 1 0 0 1 0 0 1 0 1 1 0 0 1 0 1 2 2 - 0 1

congesta
0 1 1 0 0 2 - 1 2 1 1 0 1 1 0 2 - 1 0 0 0 1 0 0 0 0 0 0 6 1 0 2 0 0 0 - 1 - 0 - 1 0 0 0 2 1 0 0 0 1 0 1 2 1 0 0 1

madagascariensis
1 0 1 1 - 0 1 0 1 1 2 1 1 0 0 0 0 0 1 0 0 0 0 1 0 0 ? 0 0 0 2 0 0 0 0 1 1 0 0 2 1 1 0 1 1 1 0 0 2 1 1 0 1 0 1

tisserantii
1 0 1 1 - 2 0 0 2 1 2 1 2 2 0 0 5 0 1 1 0 1 0 1 1 0 1 0 0 0 1 0 0 0 1 1 0 0 2 1 1 1 0 0 1 0 1 1 0 0 1 0 1 0 1

latialata
1 0 1 1 - 0 1 0 1 1 2 1 1 0 1 0 1 0 0 0 1 0 1 1 0 0 1 0 1 1 0 1 0 1 0 1 1 0 0 2 1 1 1 0 0 1 0 1 1 0 1 0 1 0 1

geelvinkiana
1 0 1 1 - 0 1 0 1 1 2 1 ? 0 0 0 ? 0 0 3 0 0 0 0 0 5 0 0 0 0 0 ? 1 ? 1 1 0 2 ? ? ? 1 0 ? ? 1 0 1 0 1 0 1 0 1

cochinchinensis
1 0 1 1 - 0 1 0 1 1 2 1 1 0 0 0 1 0 1 0 1 0 1 0 1 0 1 0 1 4 1 0 2 0 0 0 0 1 ? ? 1 1 0 2 1 1 0 1 0 1 0 1 0 1

bancana
1 0 1 1 - 0 1 0 1 1 2 1 ? 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0 0 2 1 1 0 1 0 0 1 0 1 0 1 0 1 1 1

disticha
0 0 1 0 1 0 0 0 0 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 0 2 1 0 0 0 6 1 0 0 0 0 2 1 1 0 1 0 0 2 1 0 0 2 1 1 0 1 1 1

coelestis
0 0 1 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 3 1 0 2 0 0 6 1 0 0 0 0 1 0 1 0 0 1 0 0 2 1 1 0 2 1 1 1 1

ledermannii
1 0 1 1 - 0 1 0 1 1 2 ? 1 0 0 0 0 1 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 1 0 1 0 0 2 1 1 0 1 0 0 1 0 1 1 0 1 0 1 0 1

connata
1 0 1 1 - 0 1 0 1 1 2 1 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 1 0 0 ? 0 0 - 1 0 ? 0 0 - 1 - 0 1 0 1 0 1

subcoelestis
1 0 1 1 - 0 1 0 1 1 2 1 1 0 0 0 0 0 1 0 1 0 0 0 0 1 0 0 0 0 0 0 ? 1 0 1 0 0 2 1 1 0 1 0 0 ? 1 0 0 2 1 1 1 1

luteoalba
1 0 1 1 - 0 1 0 1 1 2 1 1 0 0 0 0 0 0 0 0 0 0 0 4 1 0 0 0 0 0 0 0 1 0 1 0 0 2 1 1 0 1 0 0 1 0 1 0 1 0 1 0 1

juncea
1 0 1 1 - 0 1 0 1 1 2 1 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 1 0 0 ? 1 0 0 0 1 0 0 ? 1 0 0 1 1 0 1 0 1

sphagnoides
0 1 1 0 2 1 0 1 2 1 1 3 2 1 0 2 - 0 0 0 1 0 0 1 1 0 1 0 0 0 2 0 0 3 0 1 0 0 1 1 0 0 1 1 0 1 1 0 0 2 2 0 0 1

engganensis
0 1 1 0 2 1 0 1 1 0 1 1 0 2 - 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 0 0 0 - 1 0 - 0 - 1 0 0 0 0 1 0 1 0 1

championii
0 1 1 ? ? 2 - 1 2 1 1 0 1 1 0 2 - 0 0 0 0 1 0 0 1 0 0 0 ? 1 0 2 0 0 0 - 0 - 0 - 1 0 0 1 0 1 0 1

0 1 1 0 0 2 - 1 2 1 1 0 ? 1 0 2 - 0 1 0 1 0 0 0 0 0 1 0 0 0 6 1 0 2 0 0 0 - 0 - 0 - 1 0 1 2 1 0 0 1

Table 1 (continued)

Taxon	Character states
micropetala	0 1 1 1 - 2 - 1 2 1 1 1 2 1 0 2 - - 0 0 1 0 0 0 0 1 0 0 0 0 6 1 0 2 0 0 0 0 0 1 0 1 0 - - - 0 1 0 - 0 0 1 2 1 0 0 1
oblonga	2 1 1 1 - 2 - 1 2 1 3 1 2 2 0 0 3 0 0 0 0 1 0 0 0 1 0 2 0 0 - 1 - - 2 1 3 1 1 0 0 1 0 2 0 2 1 3 1 1 0 0 0 0 0 0 1
wallichii	1 1 0 1 - 2 - 1 2 1 3 1 2 2 0 0 0 0 0 0 0 1 0 1 0 0 0 3 1 0 0 0 0 0 1 0 0 0 1 1 1 0 0 2 1 0 1 0 1 1 0 1 1 0 1 0 1
cryptopetala	0 1 1 0 1 2 - 1 2 1 3 0 2 ? 0 0 4 1 0 0 0 - 0 1 1 0 0 0 0 0 - 1 - - 0 1 3 1 1 0 0 1 0 0 0 1 0 0 1 0 0 1 0 1 0 1
candida	1 1 1 1 - 2 - 1 2 1 3 1 2 2 0 0 3 0 0 1 0 1 1 0 1 1 0 0 0 0 1 1 0 0 0 2 0 1 1 0 0 1 1 0 0 1 1 0 0 1 0 1 0 1
lutescens	1 1 1 1 - 2 - 1 2 1 3 1 ? ? 0 0 4 2 0 0 0 1 0 1 1 0 1 0 0 0 0 1 0 0 0 1 1 0 0 1 2 0 1 1 0 0 1 1 0 0 0 0 0 0 1
malasica	1 1 1 1 - 2 1 1 2 1 3 1 2 2 0 0 0 0 0 1 0 1 0 1 0 0 0 3 1 ? 0 0 0 7 0 0 1 1 0 0 7 1 1 0 0 0 ? 1 1 0 0 0 0 0 0 0 1
itoana	1 1 1 1 - 2 1 1 2 1 3 1 2 0 0 0 0 0 1 0 1 0 1 0 0 0 0 5 0 0 0 0 0 0 1 1 0 0 0 1 1 0 0 0 - 1 0 1 1 0 1 0 1
nepalensis	0 1 0 0 1 2 - 1 2 1 3 0 2 ? 0 0 4 1 0 0 0 1 0 1 1 0 0 2 0 2 3 1 0 0 0 2 1 3 1 1 0 0 - 1 0 0 1 0 1 0 1
stricta	1 1 1 0 - 2 - 1 2 1 3 1 2 ? 1 0 7 0 1 1 0 1 0 1 0 0 1 0 3 1 0 0 0 0 1 2 0 2 0 0 1 1 7 0 1 0 0 0 0 0 0 1
candelabrum	1 1 ? 1 - 2 - 1 2 1 3 1 2 2 0 0 0 0 0 0 0 1 0 1 1 0 0 0 5 0 0 0 ? 7 0 0 2 1 1 0 1 1 1 0 0 1 0 1 0 1
indica	1 1 ? 1 - 2 - 1 2 1 3 1 1 0 0 0 1 0 0 0 0 1 0 1 0 0 0 0 6 1 0 0 0 0 0 1 1 0 1 1 0 1 1 1 0 0 1 0 1 0 1
chinensis	1 1 ? 1 - 2 - 1 2 1 3 1 1 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 1 0 0 2 0 1 1 0 1 1 0 1 0 1 0 1
filamentosa	1 0 1 0 1 2 1 1 0 0 0 0 0 0 0 1 0 1 0 3 0 0 0 1 0 1 0 0 0 0 1 1 1 0 0 1 1 0 1 1 1 0 1 1 1 0 1 1 1
gracilis	1 0 1 0 1 2 1 ? 0 0 0 0 0 0 0 0 1 0 1 ? 0 0 0 0 1 0 0 0 2 0 1 0 0 0 - 1 0 0 1 0 0 1 1 0 1 0 1 1 1
larseniana	1 1 1 1 - 2 1 2 3 0 1 0 0 0 0 0 0 0 0 0 1 0 1 ? 1 0 0 6 1 0 2 0 0 0 1 1 0 0 1 1 0 0 1 0 0 1 0 0 0 1
occidentoindica	1 0 1 1 - 2 - 1 2 1 2 1 2 2 0 0 1 0 0 1 0 0 1 0 0 0 1 3 1 0 0 0 1 0 1 1 0 0 0 1 1 0 0 1 0 1 0 1 1 1
pusilla	1 0 1 1 - 0 1 0 1 1 2 1 2 2 0 0 1 0 0 1 0 1 0 0 0 0 6 0 0 2 0 0 1 0 1 1 0 0 2 0 1 1 1 0 0 1 1 1

1.2　Characters and scoring of states

Sixty-one morphological characters were coded as "Non-additive" or "Unordered" in this analysis. These characters include 12 vegetative characters, 45 reproductive characters, and 4 seed characters. The characters and the scoring of states for these characters are as following:

1. Perennial herb (0); short-lived annual herb (1).
2. Plant chlorophyllous (0); achlorophyllous (1).
3. Plant with bluish or purplish pigments (0); without such pigments (1).
4. Rhizome present (0); absent (1).
5. Rhizome globose (0); creeping cylindrical (1); erect cylindrical (2).
6. With well-developed basal rosette leaves (0); with distichous basal leaves (1); without basal leaves (2).
7. Basal and stem leaves similar in size (0); readily distinguishable (1).
8. Leaf linear ensiform or lanceolate (0); triangular or scale-like (1).
9. Leaves longer than 3 cm (0); usually 0.8 ~ 2.5 cm (1); not more than 0.5 cm (2).
10. Leaves wider than 0.5 cm (0); not wider than 0.3 cm (1).
11. Leaf veins: many (0); 5 ~ 7 (1); 3 (2); 1 (3).
12. Stem robust, radius > 3 mm (0); stem slender, < 2 mm (1).
13. Stem longer than 35 cm (0); longer than 15 cm but not exceeding 30 cm (1); not exceeding 15 cm (2).
14. Inflorescence a double cincinnus (0); a head (1); reduced to 1 or 2 flowers (2); multi-cincinni (3).
15. Inflorescence with erect flowers (0); with hanging flowers (1).
16. Flowers with 3 prominent perianth wings (0); wings reduced to 3 ribs (1); neither wings nor ribs present (2); perianth with 6 ribs (3).
17. Perianth wings half-elliptic or half-orbiculate (0); half-obovate (1); half-ovate (2); half-oblong (3); half-cuneate (4); obo-hastate (5).
18. Perianth wings wider than perianth tube (0); not so (1).
19. Perianth tube cylindrical (0); triangular (1).
20. Perianth tube longer than ovary (0); not so (1).
21. Perianth tube straight (0); curved (1).
22. Outer and inner perianth lobes with equal length (0); with different length (1).
23. Perianth lobes persistent (1); caducus (1).
24. Outer perianth lobes triangular (0); ovate (1); oblong (2).
25. Outer perianth lobes apex acute (0); obtuse (1); emarginate (2).

26. Outer perianth lobes with single margins (0); with double margins at base (1); with a high ridge parallel to the margin (2); with shallow double margins (3); with prominently double margins (4).
27. Outer perianth lobes erect flat (0); margin involute (1); revolute (2).
28. Outer perianth lobes apex erect (0); apex revolute (1).
29. Outer perianth lobes not thickened (0); margin thickened (1); whole perianth lobe thickened (2).
30. Outer perianth lobes length > width (0); length < width (1).
31. Outer perianth lobes not connate (0); connate and enclosing the inner perianth lobes (1); connate above the inner lobes (2).
32. Inner perianth lobes triangular (0); ovate (1); oblong (2); orbicular (3); spathulate (4); linear (5); elliptical (6).
33. Inner perianth lobes apex acute (0); obtuse (1).
34. Inner perianth lobes present and persistent (0); absent (1).
35. Inner perianth lobes erect flat (0); margin involute (1); revolute (2).
36. Inner perianth lobes with single margins (0); with double margins (1); with high ridges parallel to the margin (2).
37. Inner perianth lobes not swollen (0); swollen (1).
38. Flower length: always less than 1 cm (0); usually 1 ~ 1.5 cm (1); always longer than 1.5 cm (2).
39. Flower color (perianth tube and wing): without violet or purplish pigments (0); with such pigments (1).
40. Flower color (perianth lobes): without yellowish pigments (0); yellowish (1).
41. Flower color (perianth lobes): without bluish/purplish pigments (0); with such pigments (1).
42. Pedicel: flower sessile or subsessile (0); with short pedicels (1); pedicel longer than ovary (2).
43. Bract: shorter than flower (0); longer than flower (1).
44. Perianth wing: running from the middle of lobes (0); from the apex of lobes (1); from the base of lobes (2).
45. Perianth wing: running to below the base of ovary (0); to the middle of ovary (1); to the apex of

ovary (2).

46. Ovary globose or subglobose (0); obovoid (1); ellipsoid (2); rhomboid (3).
47. Stamen with filament (0); without filament (1).
48. Anther connective without an apical divergent crest (0); with an apical divergent crest (1).
49. Anther connective apical crests 'Y-shaped' (0); with the connective 'T-shaped' (1).
50. Anther connective apical crests shorter than the thecae (0); as long as or longer than the thecae (1).
51. Anther connective hanging spur absent (0); with one hanging spur (1); with two divergent spurs (2).
52. Anther connective hanging spurs acute (0); obtuse (1).
53. Anther connective hanging spurs shorter than the thecae (0); as long as or longer than the thecae (1).
54. Anther connective with an acute appendage on the middle pointing toward the style (0); without such structure (1).
55. Stigma sessile (0); on short style branch (1).
56. Style thick-filiform (0); slender (1).
57. Seed elongated fusiform (0); ellipsoid (1); triangular globose or subglobose (2).
58. Seed surface: striate (0); reticulate (1); irregular (2).
59. Seed surface: with thin and sharp ridges (0); with thick and rounded ridges (1).
60. Seed surface: Ridges not beaded (0); ridges beaded (1).
61. Placenta lateral (0); axil (1).

1.3   Cladistic analysis

All analyses were run on an IBM-compatible 486 computer and a Macintosh Power PC. The software used was Hennig 86 ver.1.5 (Farris, 1989) (to get the shortest trees) and PAUP 3.1 (Swofford, 1991) (to produce cladograms longer than the shortest trees to be used in testing tree robustness by topology decay). Although an implicit enumeration (ie) of the data may result in trees with the minimal length, it is time-consuming with larger data-sets. It was aborted after an analysis of the present data-set had not completed after two weeks. Instead, the command "bb ∗", which applies extended branch-swapping to the trees in current tree file, producing a new file, and retains the shortest trees. The commands and settings in PAUP searching are heuristic searching; simple addition sequence; tree-bisection-reconnection (TBR) branch-swapping performed; branches having maximum length zero collapsed to yield polytomies.

All characters are coded as "non-additive" (Hennig 86) or "unordered" (PAUP). Polymorphic and uncertain character states were coded as "?", while "-" indicates that the character is inapplicable to the taxon.

The topology decay (Bremer, 1988) in cladograms longer than the most parsimonious ones is a routinely used indicator of the robustness of the clades in the most parsimonious cladograms. It has been practiced in the phylogenetic analysis of diverse groups (e.g., Baum et al., 1994) and has been employed in the present study. The cladograms one step longer than the most parsimonious ones were searched and retained by using PAUP with the same settings as specified above. Instead of retaining only the shortest trees, trees longer than those trees as found in previous runnings were retained.

2   Results

2.1   Corsiaceae as outgroup

The dataset running on Hennig 86 with the command "bb" produced 100 most parsimonious cladograms of 460 steps long (Fig. 1) with subsequent trees overflowing. The strict consensus tree (Fig. 2) is comparatively well resolved. The same dataset using PAUP with the "heuristic searching" produced 2503 shortest trees of 461 steps. The consistency index (CI) is 0.215 and the retention index (RI) is 0.625 respectively.

As accompanying the loss of chlorophyll, a series of vegetative characters are supposed to
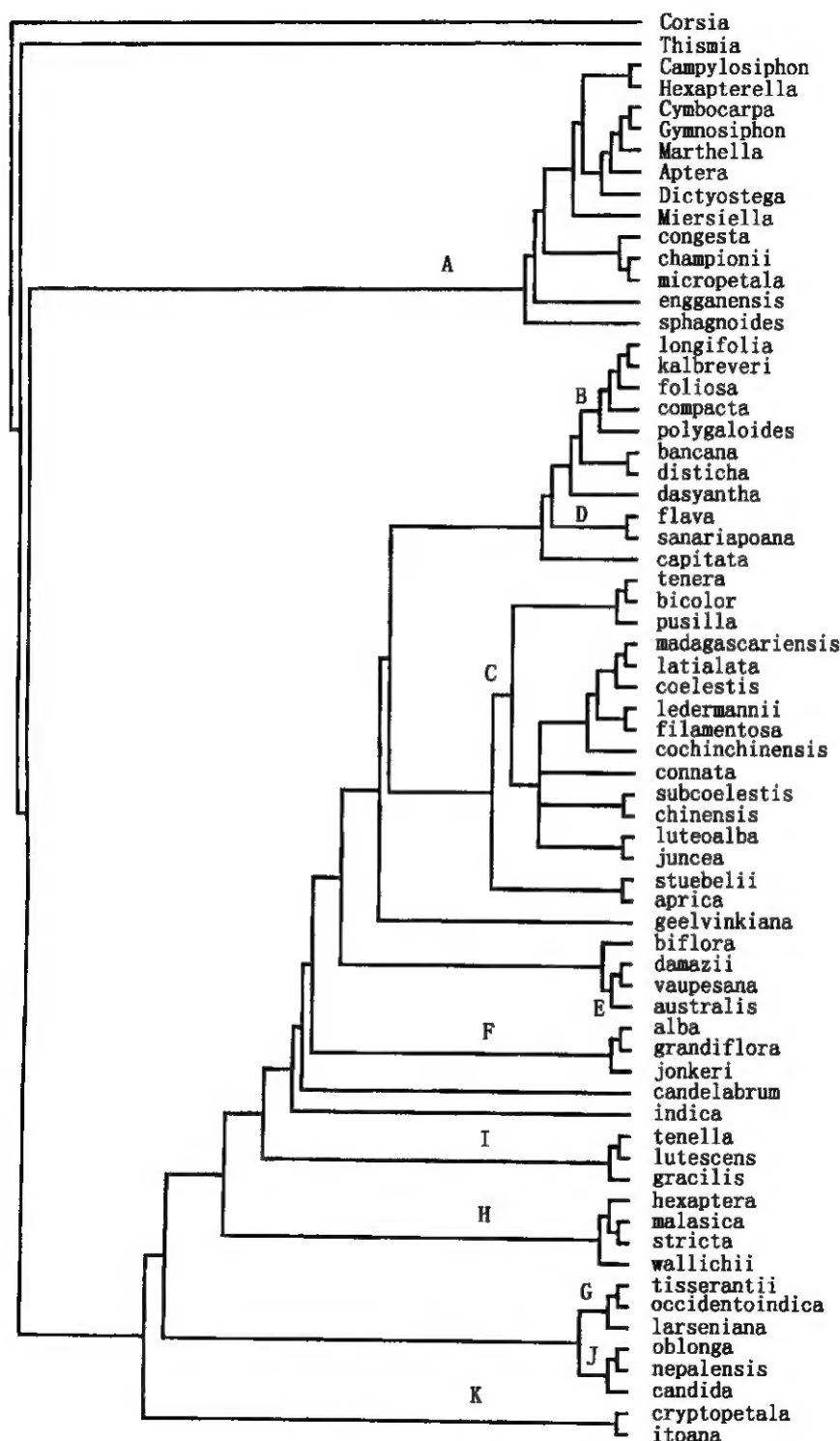
Fig.1   One of the 100 most parsimonious cladogram with *Corsia* as the outgroup (Hennig 86 "bb"). Letters (A, B, C, etc.) correspond to the clades mentioned in the paragraphs above. Tree length 460.
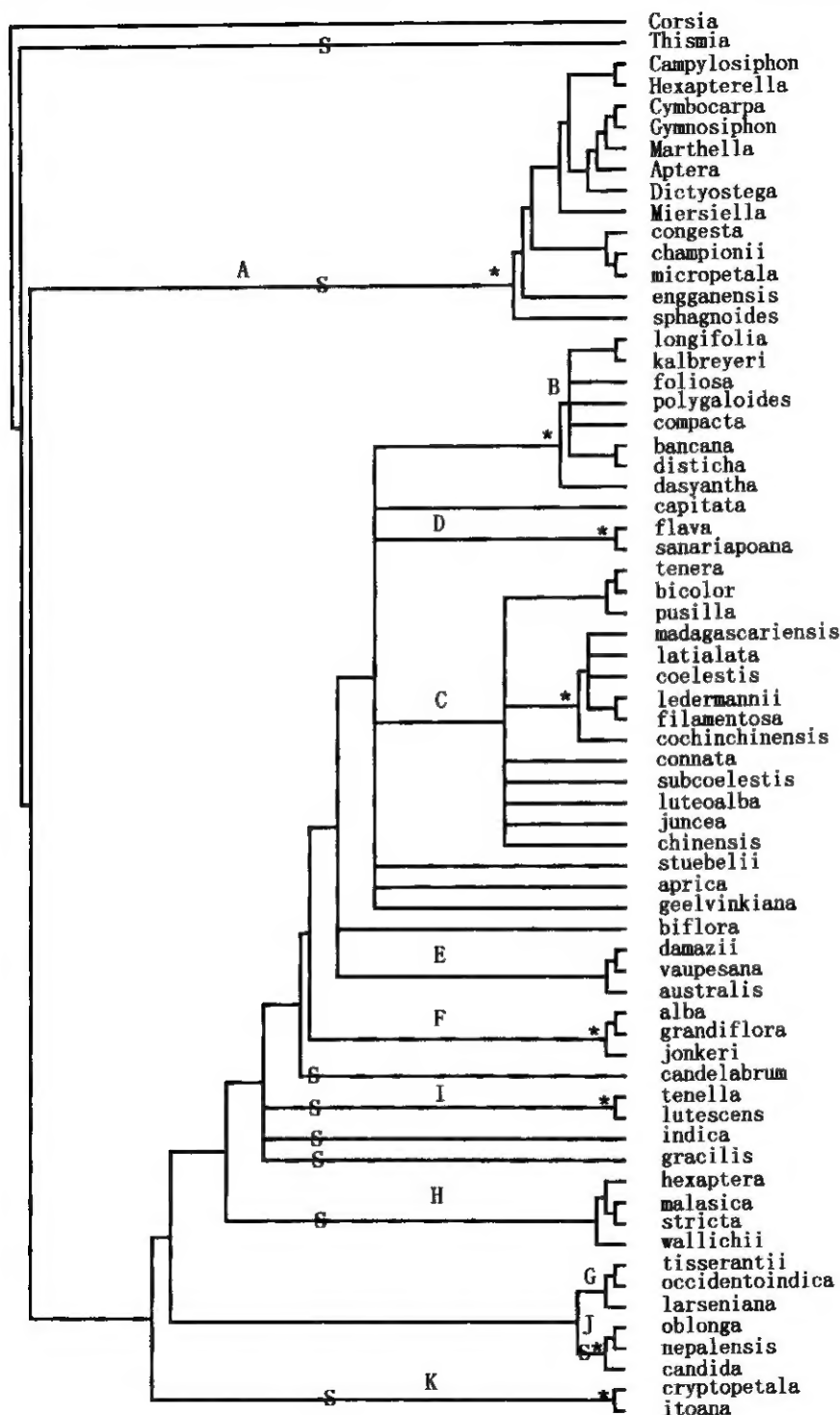
Fig. 2　Strict consensus cladogram of the 100 most parsimonious trees with *Corsia* as outgroup (Hennig 86 "bb * "). The mycotrophic clades are indicated by a "S", while the clades surviving in the strict concensus tree of 2503 trees one step longer (461 steps) than the most parsimonious cladograms are indicated by a " * ".

change (Leake, 1994), and the cladograms produced may have been affected by the convergent evolution of vegetative characters, an analysis with the vegetative characters deleted from the data matrix is important, and might be a more objective test of the emergence of holo-mycoheterotrophism. To limit the influence of vegetative characters on the topology of cladograms, the seven leaf characters (characters 2, 6 ~ 11) were excluded from the analysis. The Hennig 86 command "bb" produced 54 shortest trees of 419 steps long with the consistency and the retention indices at 0.21 and 0.58 respectively. The PAUP running with the "heuristic searching" in effect failed to find trees that were as short or shorter. The strict consensus of these 54 trees (Fig. 3) is essentially similar to the one with all the characters included in terms of the positions of most of the *Burmannia* taxa, as the mycotrophic species are still the earliest to be branched and the robust species are among the latest.

In all the most parsimonious cladograms produced (Fig. 1) and its strict consensus tree (Fig. 2), the *Thismia* clade is basal. The remaining taxa split into two clades: one clade (clade A) includes five *Burmannia* species without perianth wings and eight genera in the tribe Burmannieae of the family Burmanniaceae (Fig. 4). Taxa in this clade share a series of synapomorphies including many-veined leaves which are distinct from other mycotrophic species which have single-veined leaves; absence of perianth wings; and the connective with an inwardly oriented median appendage. Seed morphology of these genera as studied by Rübsamen (1986) also revealed their similarity with species without perianth wings in the genus *Burmannia* in having more or less globose or subglobose seeds with oblong or tetragonal epidermal cells while all other species in the genus *Burmannia* and species of *Thismia* have seeds with narrow, spirally arranged epidermal cells. Ecologically, taxa in this clade are usually found in wet, humus-rich forest floors under thick forests. *Burmannia sphagnoides* and *B. engganensis* are the basal branches in this clade, while the eight genera form a clade that is sister to the *B. championii—B. micropetala—B. congesta* clade. As revealed by the cladograms, the other genera in tribe Burmannieae probably represent a clade of more specialized taxa. The other clade includes all other species in the genus *Burmannia*.

In the clade consisting entirely of *Burmannia* species, the mycoheterotrophic species are among the earliest clades to branch off while the robust autotrophic species are among the latest to emerge in the cladograms. The chlorophyllous species of *Burmannia* except *B. larseniana*, *B. occidentoindica* and *B. tisserantii* form a monophyletic clade.

The chlorophyllous species are found in two main clades and several smaller clades: one main clade includes the five sect. *Foliosa* species, viz., *B. polygaloides*, *B. compacta*, *B. foliosa*, *B. kalbreyeri*, and *B. longifolia* (clade B, Fig. 5), which is closely related to the *B. disticha—B. bancana* clade and then the American species *B. dasyantha*, and also the *B. flava—B. sanariapoana* clade (clade D); the other main clade is the "semi-autotrophs" clade of 14 Asian-Australasian, African and American species (clade C), including *B. pusilla*, *B. chinensis*, *B. juncea*, *B. luteo-alba*, *B. subcoelestis*, *B. connata*, *B. cochinchinensis*, *B. filamentosa*, *B. ledermannii*, and *B. coelestis*, and two species, *B. bicolor*, and *B. tenera* from the Americas, and the other two species, *B. madagascariensis* and *B. latialata* from Africa, form another clade (clade C, Fig. 6). Species in this clade are usually found in open, wet habitats of the American "wet savanna" or African "Inselbergs" or Asian " wet grassy places", and are associated with *Eriocaulon* sp., *Xyris* sp., etc.

Other chlorophyllous clades found in the strict consensus tree include: clade D——— the clade
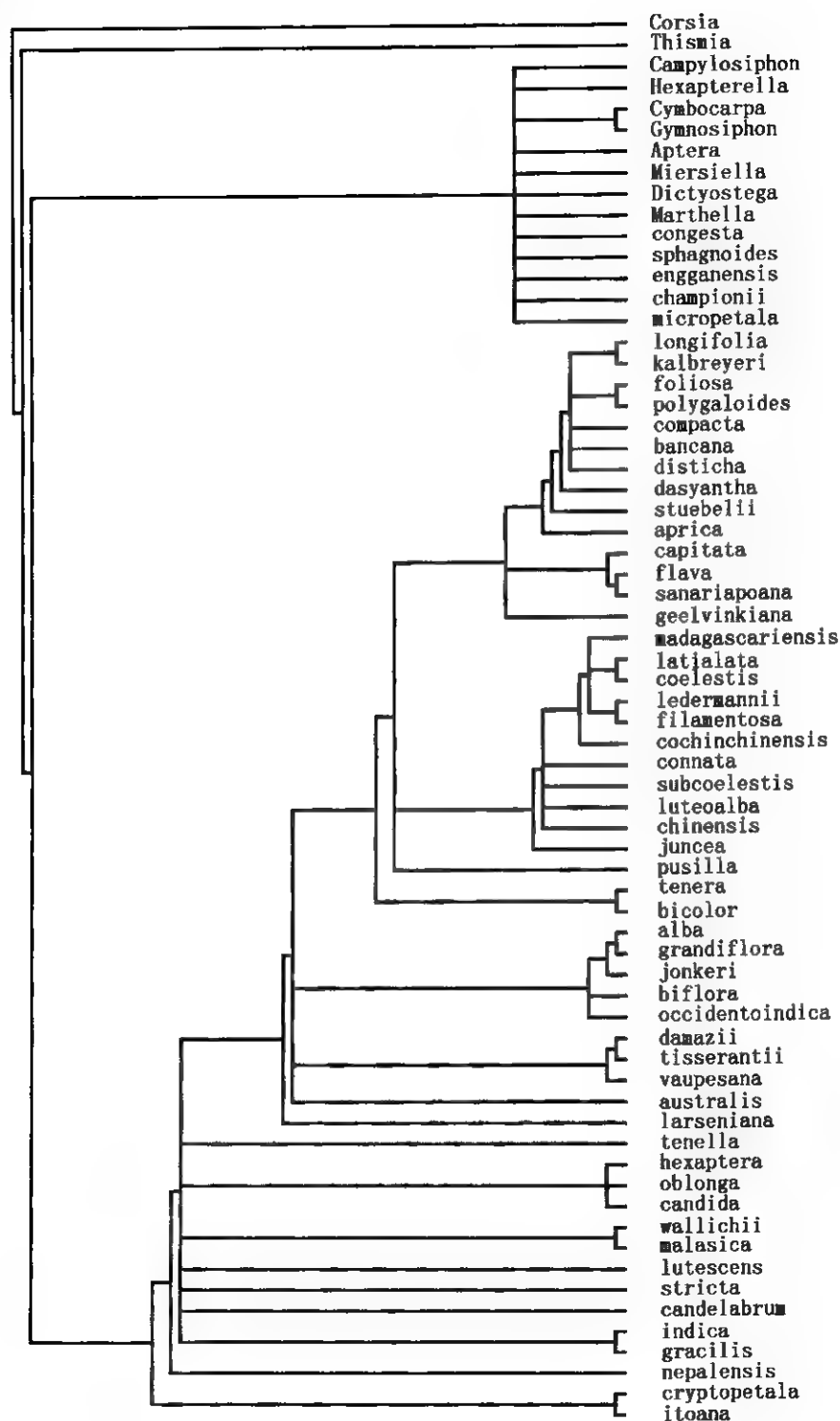
Fig. 3   Strict consensus cladogram of the 54 most parsimonious trees of *Burmannia* with *Corsia* as outgroup and 7 leaf characters deleted (Hennig 86 "bb＊"). Tree length 419.
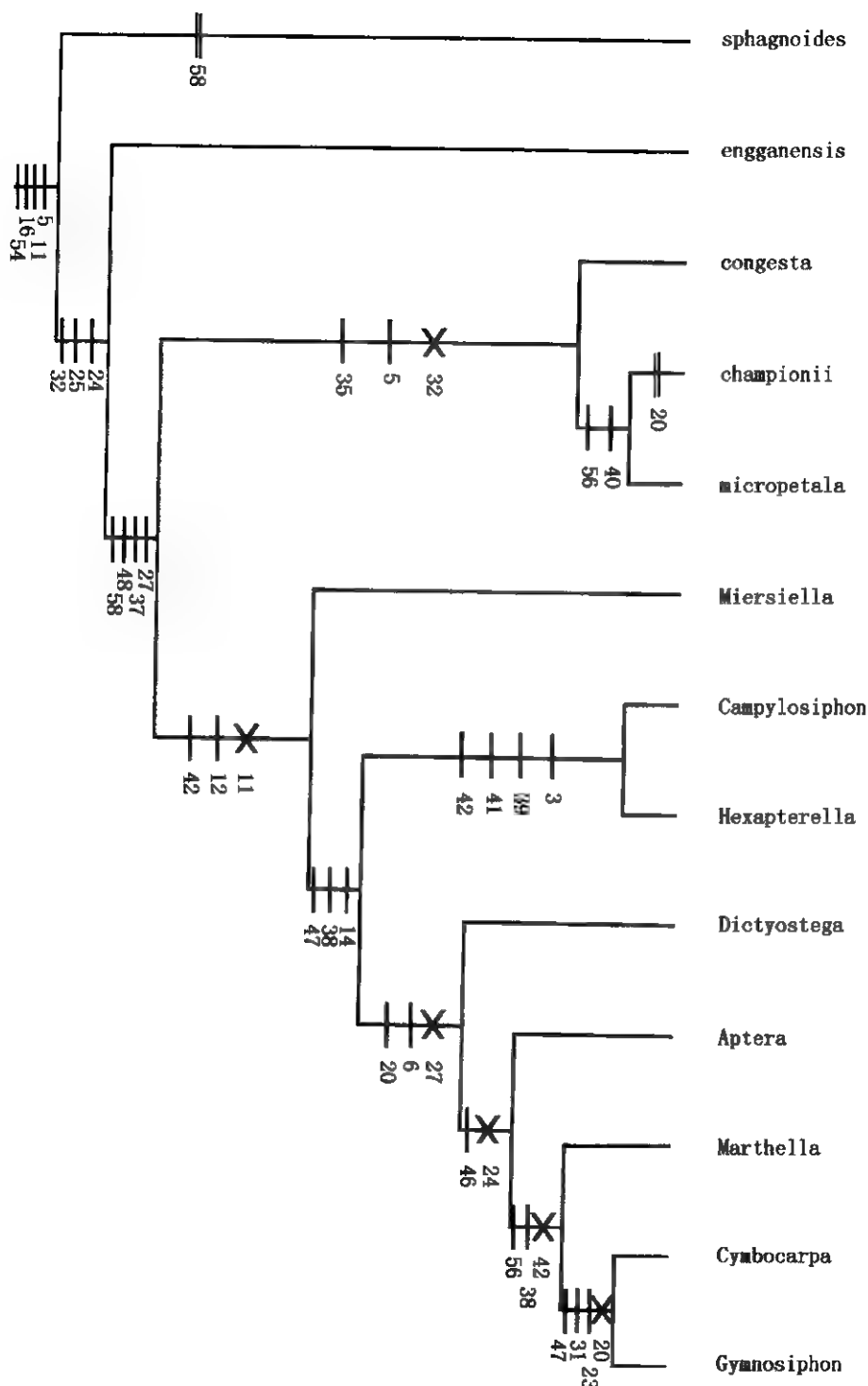
Fig. 4　The "wingless" clade of 13 OTUs. The clade is defined by four apomorphies (characters 5: 1→2; 11: 3 →1; 16: 0→2; 54: 1 →0).
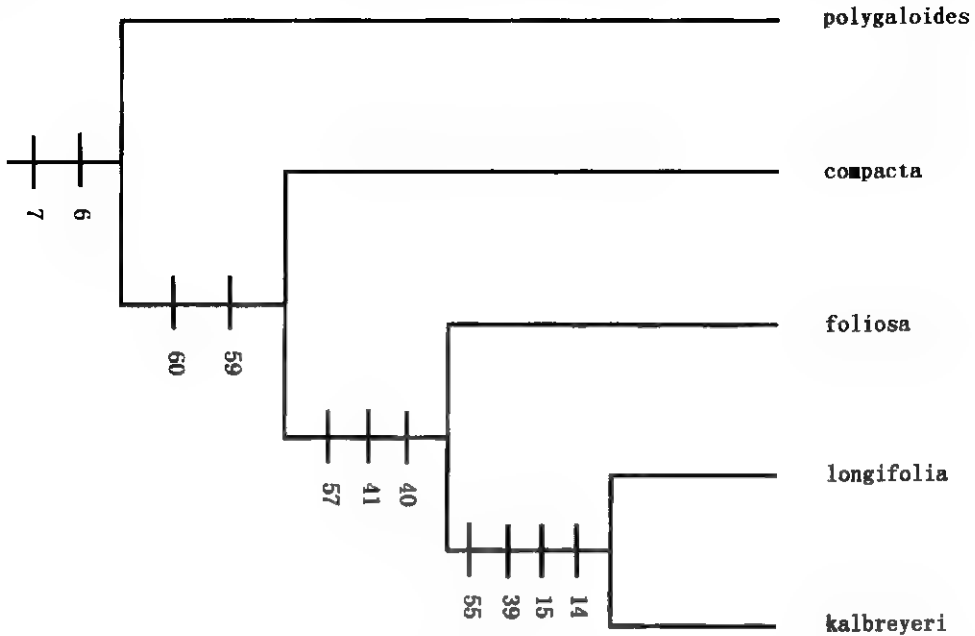
Fig.5 The "Foliosa" clade of 5 species: *B. polygaloides*, *B. compacta*, *B. foliosa*, *B. kalbreyeri* and *B. longifolia*. The clade is defined by two apomorphies (characters 6: 0→1; 7: 1→0).

of two American "semi-mycotrophic" species, *B. flava* and *B. sanariapoana*; clade E—— the clade of three American green-leaved species, *B. australis*, *B. vaupesana*, and *B. damazii*; clade F—— the American clade of green leaved species, *B. jonkeri*, *B. alba*, and *B. grandiflora*; clade G—— the clade of three highly reduced "semi-mycotrophs" from Asia and Africa, *B. larseniana*, *B. occidentoindica*, and *B. tisserantii*. The phylogenetic relationships of *B. capitata*, *B. stuebelii*, *B. aprica*, and *B. geelvinkiana* are not fully resolved.

The achlorophyllous species (other than the "wingless taxa") are found in the following clades: clade H—— the clade that includes four "tiny mycoheterotrophs" from Asia and Africa, *B. wallichii*, *B. hexaptera*, *B. stricta* and *B. malasica*; clade I—— the clade of the Malesian species *B. lutescens* and the Neotropical species *B. tenella*, which is most probably related to the Malay and Thai Peninsula species *B. gracilis*; clade J—— the clade of three Asian mycoheterotrophic species, *B. candida*, *B. nepalensis*, and *B. oblonga*; and clade K—— the clade of two east Asian mycoheterotrophic species, *B. itoana* and *B. cryptopetala*. The relationships of two Indian achlorophyllous species, *B. candelabrum* and *B. indica*, are not resolved.

2.2 Orchidaceae as outgroup

If a chlorophyllous representative species of the family Orchidaceae (*Habeneria* sp.) is chosen as outgroup, and the ingroup includes the same terminal taxa, the cladistic analysis using all 61 characters in the Hennig 86 command "bb" produced 100 shortest trees and overflowed. The trees (Fig. 7) are 453 steps long with a CI of 0.21 and a RI of 0.63. The strict consensus tree (Fig. 8) is topologically reversed from the cladograms produced using the Corsiaceae as outgroup: the basal branches are the robust *Burmannia* species with well-developed green leaves, while the mycoheterotrophic species are among the last to branch off.

Species of the sect. *Foliosa* are again found in a single clade (clade B) in some of the cladograms produced (Fig. 7), although their relationships are not resolved in the strict consensus tree (Fig. 8). The "semi-mycotrophs" clade of 14 Asian-Australasian, African and American species (clade C) remains the same as in the cladograms of the previous running. The *B. disticha—B. bancana* clade, the American species *B. dasyantha*, *B. flava*, *B. sanariapoana*, together with the species in sect. *Foliosa* are among the basal branches of the cladogram. *Burmannia larseniana*, *B. tisserantii*, *B. occidentoindica*, and *B. biflora* are the species most closely related to the clade of all mycoheterotrophic species. The mycoheterotrophic taxa form a monophyletic group with the clade of three Asian mycoheterotrophic species, *B. candida*, *B. nepalensis* and *B. oblonga* (clade J) being the first to branch off.

Thismia is joined in a clade including all the mycoheterotrophic taxa. It is the sister group of the "wingless" clade (clade A). The other genera of Burmanniaceae are again found in the "wingless" clade identical to the one in the trees with *Corsia* as outgroup (clade A, Fig. 4). *Thismia* and the "wingless" clade collectively form the clade that is the sister group of the clade of two Eastern Asian mycoheterotrophic species, *B. itoana* and *B. cryptopetala* (clade K).

The *B. indica—B. candelabrum* clade is sister to the *B. tenella—B. lutescens—B. gracilis* clade (clade I). These five species in turn form a clade that is sister to the "tiny mycoheterotrophs" clade (clade H). This main clade is sister to the clade of the "wingless taxa" (clade A) and the clade of two East Asian mycoheterotrophic species, *B. itoana* and *B. cryptopetala* (clade K) combined.

2.3 Test of cladogram robustness

The decay of cladograms produced with *Corsia* as outgroup was tested by comparing the strict consensus cladogram of 100 "bb" trees of 460 steps long (Fig. 2) with the strict consensus tree of 2503 PAUP "heuristic" trees of 461 steps long. The clades surviving in the latter are marked with an asterisk.

The decay of cladograms with Orchidaceae as outgroup was tested using the same techniques. The strict consensus tree (Fig. 8) of 100 "bb" trees of 453 steps long was compared with the strict consensus tree of 7800 PAUP "heuristic" trees of 456 steps long, which are the shortest trees produced, and which are 3 steps longer. The clades of figure 8 that survived in the latter are also marked with an asterisk.

In the strict consensus tree derived from the cladograms one steps longer than the most parsimonious cladograms with *Corsia* as outgroup, the whole "wingless" clade, viz., the clade that includes all other genera in tribe Burmannieae and the mycotrophic species without perianth wings survived. Other clades that survived include: the clade of sect. *Foliosa* species plus *B. dasyantha*, *B. disticha* and *B. bancana*; the clade of *B. alba*, *B. grandiflora* and *B. jonkeri*; a subclade of the "semi-mycotrophs" clade, including *B. cochinchinensis*, *B. filamentosa*, *B. ledermannii*, *B. coelestis*, *B. madagascariensis* and *B. latialata*; the clade of three Asian mycotrophic species, *B. candida*, *B. nepalensis*, and *B. oblonga*; and the clade of two Eastern Asian mycotrophic species, *B. itoana* and *B. cryptopetala*.

The strict consensus tree of the cladograms three steps longer (the shortest trees that PAUP can find) than the most parsimonious cladograms using Orchidaceae as outgroup is topologically similar to the strict consensus tree of the 100 "bb" shortest trees, although fewer clades survived than in the cladograms one steps longer using *Corsia* as outgroup. The clades that survived include: the whole
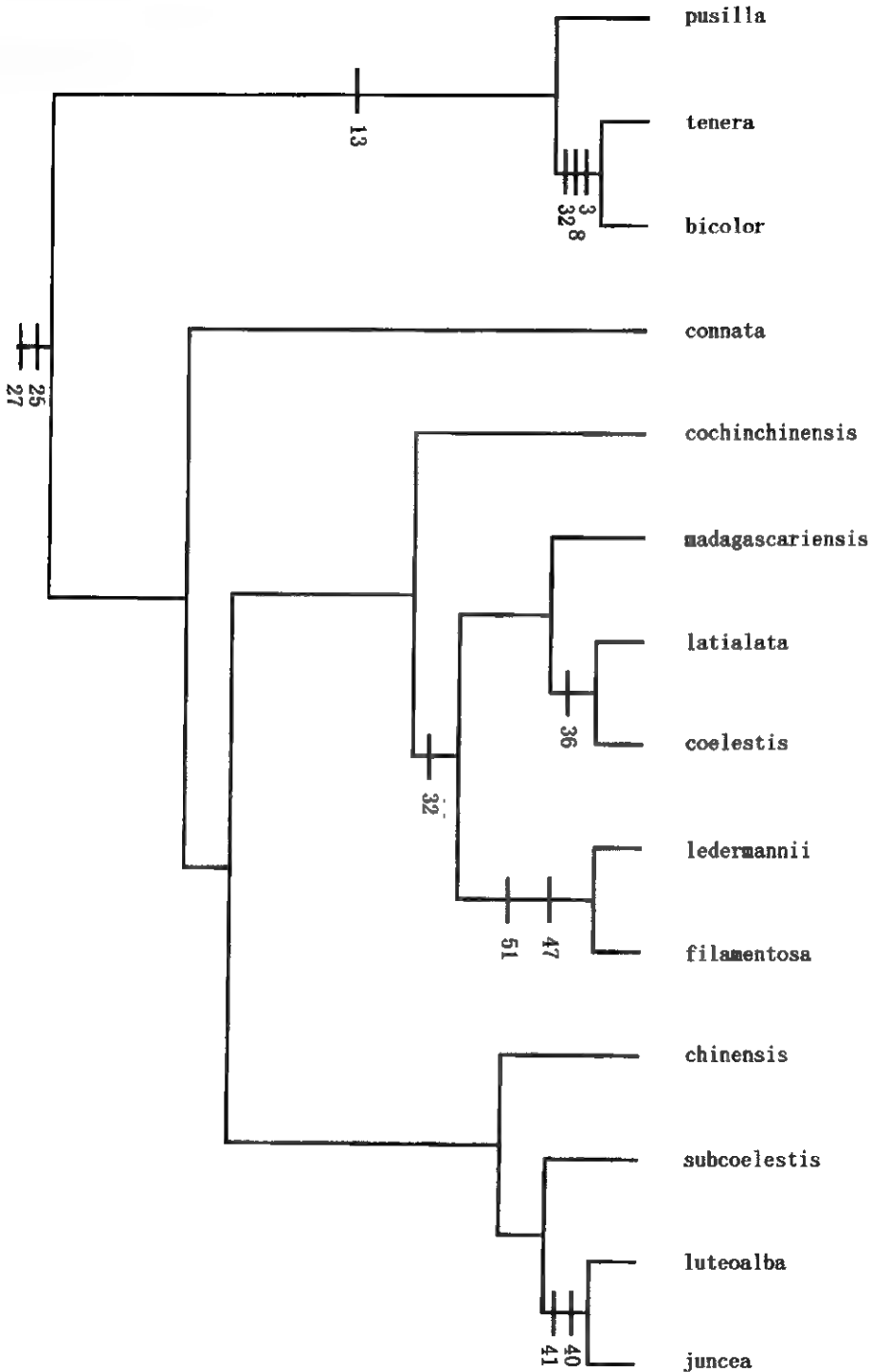
Fig.6 The "semi-autotrophs" clade of 14 species: *B. pusilla*, *B. chinensis*, *B. juncea*, *B. luteo-alba*, *B. subco-elestis*, *B. connata*, *B. cochinchinensis*, *B. filamentosa*, *B. ledermannii*, *B. coelestis*, *B. bicolor*, *B. tenera*, *B. madagascariensis* and *B. latialata*. The clade is defined by two apomorphies (characters 25: 1 →0; 27: 1 →0).
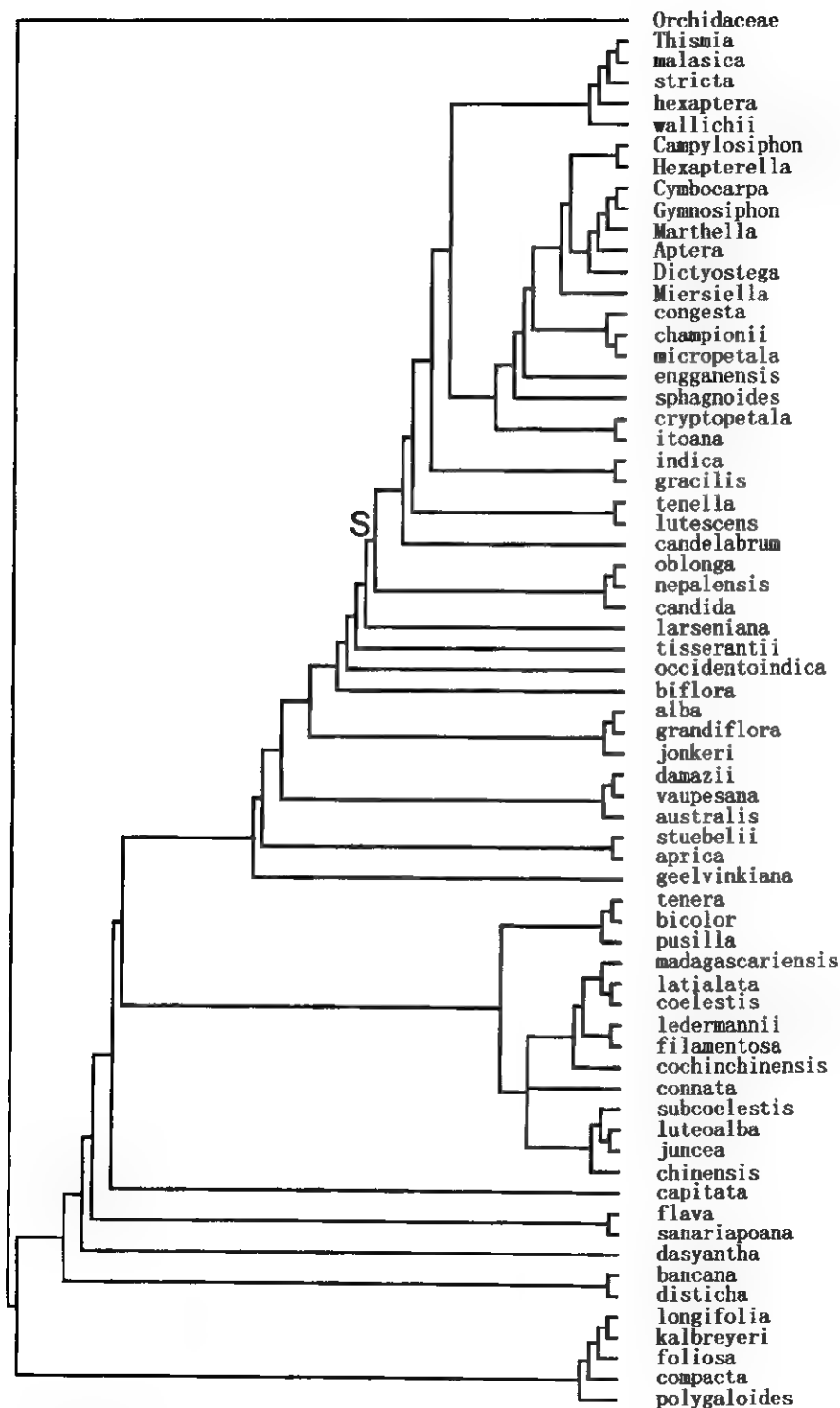
Fig. 7   One of the 100 most parsimonious cladogram with the Orchidaceae as outgroup (Hennig 86 "bb"). Tree length 453 steps. The mycotrophic clade is indicated by a "S".

Orchidaceae
Thismia
Campylosiphon
Hexapterella
congesta
championii
micropetala
sphagnoides
engganensis
Miersiella
Cymbocarpa
Gymnosiphon
Aptera
Dictyostega
Marthella
cryptopetala
itoana
tenella
lutescens
candelabrum
indica
gracilis
hexaptera
wallichii
malasica
stricta
oblonga
nepalensis
candida
larseniana
tisserantii
occidentoindica
biflora
alba
grandiflora
jonkeri
damazii
australis
vaupesana
capitata
tenera
bicolor
pusilla
madagascariensis
latialata
coelestis
ledermannii
filamentosa
cochinchinensis
connata
subcoelestis
chinensis
stuebelii
aprica
geelvinkiana
luteoalba
juncea
flava
sanariapoana
dasyantha
longifolia
kalbreyeri
foliosa
polygaloides
compacta
bancana
disticha

Fig. 8　Strict consensus cladogram of 100 most parsimonious trees with Orchidaceae as the outgroup (Hennig 86 "bb"). The my-cotrophic clade is indicated by a "S", while the clades surviving in the strict concensus tree of 7800 trees three steps longer (456 steps) than the most parsimonious cladograms are indicated by a " * ".

of the "semi-mycotrophs" clade with 14 species; the American clade of *B. alba*, *B. grandiflora* and *B. jonkeri*; the clade of *B. disticha* and *B. bancana*; the clade of three Asian mycotrophic species, *B. candida*, *B. nepalensis*, and *B. oblonga*; and the subclade including *B. championii*, *B. micropetala*, and *B. congesta*, of the "wingless" clade.

3 Discussion and conclusion

The genus *Burmannia* is not monophyletic as the cladograms (Fig. 1 ~ 3; 7 ~ 8) revealed. The genus itself is a paraphyletic group which includes all the basal branches of the tribe Burmannieae, or even the family Burmanniaceae, although the possibility that taxa of Thismieae could be included in the Burmannieae clade is low; inclusion of *Thismia* in the mycoheterotrophic clade of *Burmannia* and other Burmannieae genera could be explained by convergence of the characters that are correlated with the loss of chlorophyll; too few characters that define the two tribes of the family Burmanniaceae are included in the present analysis because the inter-generic relationships in the Burmanniaceae is not the objective of this study.

Of the two sections recognized by Jonker (1938), sect. *Burmannia* is not a monophyletic group, although several clades of closely related species could be recognized.

In all the cladograms produced with *Corsia* or *Habenaria* as outgroup, several clades are always present. These clades include the clade of "wingless" *Burmannia* species and other genera in the tribe Burmannieae as mentioned above (Fig. 4), the "semi-mycotrophs" form a clade including 14 species distributed in the Americas, Asia-Australasia and Africa (Fig. 6), and several smaller clades.

Sect. *Foliosa* is more likely to be a monophyletic group (Fig. 5). It may have a close relationship with other robust autotrophic species in the genus: *B. dasyantha*, *B. disticha* and *B. bancana*.

Although the Corsiaceae is the sister group of the Burmanniaceae, chosing the Corsiaceae as outgroup, however, caused some problems: all three genera known in the family are mycoheterotrophs. Absence of chlorophyll and the characters correlated with it are thus treated as plesiomorphies; the cladograms produced using it as outgroup therefore have all the mycoheterotrophic taxa at the basal branches whearas the chlorophyllous taxa are found in the later derived branches. Although the achlorophyllous angiosperms also possess chlorophyll a (Cummings & Welschmeyer, 1998), the regaining of chlorophyll b in these plants have never been observed and reported.

If the evolution in *Burmannia*, or the Burmanniaceae, has been a process of loss of chlorophyll and not vice versa, the mycoheterotrophic species of the genus together with other genera in the tribe Burmannieae, if not the whole family, forms a monophyletic group, which implies that the loss of chlorophyll has only happened once, as indicated by the strict consensus tree with Orchidaceae as outgroup. The loss of chlorophyll may have happened independently in the family Corsiaceae and possibly also the tribe Thismieae.

The loss of chlorophyll is a process of many steps, correlated with the gradual decrease of complexity in vegetative organs: at the base of the cladograms are the robust autotroph species of sect. *Foliosa*, *B. disticha* and *B. bancana*; it is followed by the less robust autotrophic species, e.g., *B. dasyantha*, *B. aprica*, *B. flava*, *B. sanariopoana*, etc., and the 14 "semi-mycotrophs"; the chlorophyllous species that are related to the mycoheterotrophic clades include the species with poorly-developed basal leaves or without basal leaves at all: *B. biflora*, *B. occidentoindica*,

B. tisserantii, and *B. larseniana*.

The presence of perianth wings is a plesiomorphic character in *Burmannia*: in the cladograms produced with *Corsia* or the Orchidaceae as outgroup, the basal branches are the species with prominent perianth wings. The absence of perianth wings in the *B. sphagnoides—B. championii* group and in the other genera of the tribe Burmannieae is an apomorphic state.

The characters of size and insertion of leaves are not sufficiently important characters to warrant basing sections on them. Although there are two characters, viz., character 6 (with/without well-developed rosette leaves) and character 7 (cauline and rosette leaves indistinguishable/distinguishable), that are apomorphies and can be used in defining sect. *Foliosa*, there is no leaf character that can be used in defining sect. *Burmannia*. In fact, sect. *Burmannia* so defined (Jonker, 1938) is not a monophyletic group at all.

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摘要 以白玉簪科和兰科的代表种类分别作为外类群对水玉簪属进行了初步的分支分析。虽然运用不同外类群进行分支分析产生的结果并不完全一致,但它们均显示了属内一些稳定"支"的结构及其种间关系。分支分析还表明:水玉簪属的两个组中,*Foliosa* 组极可能是一个单系类群,而水玉簪组则是一并系类群。如果叶绿素的丧失是一个不可逆的进化过程,水玉簪族中全菌物异养习性的获得只出现过一次。

关键词 白玉簪科;水玉簪属;分支分析;腐生植物;菌物异养习性

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